

A Revision of the Ant Genus *Rhytidoponera* (Hymenoptera : Formicidae) in New Caledonia

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Abstract

In this revision of the genus *Rhytidoponera* on the island of New Caledonia, 18 species are recognized: seven previously described taxa (*acanthoponeroides* Viehmeier, *atropurpurea* Emery, *fulgens* Emery, *numeensis* André, *pulchella* Emery, *versicolor* Brown, and *wilsoni* Brown) and 11 new species (*aquila* sp.nov., *arborea* sp.nov., *depilis* sp.nov., *insularis* sp.nov., *koumensis* sp.nov., *litoralis* sp.nov., *luteipes* sp.nov., *mimica* sp.nov., *nitidiventris* sp.nov., *opaciventris* sp.nov., and *terrestris* sp.nov.). All of these species are endemic (except perhaps *terrestris*, for which there is a questionable record from Vanuatu), and they segregate into four species-groups: *acanthoponeroides* group (one species), *fulgens* group (four species), *numeensis* group (three species) and *pulchella* group (ten species). Alate queens have not been found in any species, suggesting that colonies are entirely worker-reproductive. The behaviour and nest architecture of species in the *pulchella* group indicates specialization as foliage-foragers on understorey and forest edge vegetation, in contrast to the ground-foraging tendencies of the remaining species. Some *pulchella*-group species are involved in mimicry complexes with other ants and other foliage-frequenting arthropods. Closely related species of New Caledonian *Rhytidoponera* are usually distributed allopatrically, and conspecific populations exhibit a wide range of morphological differentiation.

Introduction

The island of New Caledonia has a diverse but taxonomically unbalanced ant fauna, relative to the larger land masses of the Indo-Australian region. Several ant genera are conspicuously lacking (e.g. *Aphaenogaster*, *Podomyrma*, *Oecophylla*) or poorly represented (*Crematogaster*, *Polyrhachis*), while others have undergone considerable local radiation. Prominent in the latter category is the ponerine genus *Rhytidoponera*, of which there are at least 18 endemic species in New Caledonia. Such diversity is not evident from the taxonomic literature: Emery (1914) listed only five species of *Rhytidoponera* in his review of the New Caledonian ant fauna, and Brown (1958) recognized a total of seven species. Recent collections on the island have more than doubled the number of known species, and suggest that there has been a similar underestimation of species richness in other radiating ant genera such as *Lordomyrma*, *Chelaner*, and *Vollenhovia*.

The present revision deals with the *Rhytidoponera* species of New Caledonia, including the Loyalty Is, and is based primarily on worker ant morphology. Because there is considerable interpopulation variation, I have defined species conservatively. In general, allopatric populations have been judged conspecific unless: (1) they are at least as dissimilar as closely related, sympatric species; (2) they are not connected by known intermediate forms. Parallel electrophoretic studies of allozyme variation show that most species recognized here possess diagnostic, fixed alleles or combinations of alleles (Appendix 1). This corroborative evidence is mentioned occasionally in the text, but for the sake of utility I have based keys and species descriptions on morphological features alone.

New Caledonia appears to be the eastern limit for the genus *Rhytidoponera*, which is otherwise known from Australia, Melanesia, and adjacent islands (Brown 1958; Wilson 1958). There is a single, questionable record of the New Caledonian species, *R. terrestris*, sp. nov., from Vanuatu.

Materials and Methods

Material was examined in the following collections, with the exception of MNHU:

ANIC	Australian National Insect Collection, CSIRO, Canberra
BPBM	Bernice P. Bishop Museum, Honolulu, Hawaii
BMNH	British Museum (Natural History), London
MCSN	Museo Civico di Storia Naturale 'Giacomo Doria', Genoa, Italy
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts
MHN	Muséum d'Histoire Naturelle, Geneva, Switzerland
MNHN	Muséum National d'Histoire Naturelle, Paris
MNHU	Museum für Naturkunde der Humboldt-Universität, Berlin, D.D.R.
NHMB	Naturhistorisches Museum, Basel, Switzerland
PSW	P.S. Ward collection, University of California, Davis, California

Scanning electron micrographs were prepared with a Philips Model 501 SEM, using gold-palladium coated specimens. Particular efforts were made to avoid orthogonal or one-dimensional distortion of the micrograph, by careful positioning of the specimen on the stub and by tilt-correcting the CRT image before each photograph was taken.

Holotypes of all new species have been deposited in the ANIC; paratypes have been distributed to the BPBM, BMNH, MCZ, MNHN, and PSW.

All cited localities are listed (sometimes with variant spellings) in the gazetteer of New Caledonia published by the U.S. Board on Geographic Names (1974).

Measurements and Indices

Morphological measurements were made at 50 \times magnification on a Wild microscope, with a Nikon stage micrometer wired to an Autometrics dual-axis digital readout. All metric measurements are expressed in millimetres. Measurements were made to the nearest thousandth of a millimetre, but they have been rounded to the second decimal place.

The following measurements were taken on a large series of workers (612 in total) from all species:

HL	Head length: midline length of head proper, measured in full-face (dorsal) view, from the anterior clypeal margin to the midpoint of a line drawn across the occipital margin
ML	Mandible length: length of closed mandibles, from the anterior clypeal margin to the apices of the mandibles, <i>measured in the same plane as HL</i>
SL	Scape length: length of the first antennal segment, excluding the neck and basal condyle
ED	Eye diameter: diameter of eye, measured along its long axis in lateral view
FCD	Frontal carinal distance: maximum distance between the frontal carinae, measured in full-face (dorsal) view, anterior to the eyes (Fig. 1)
HW	Head width: maximum width of head, measured in full-face (dorsal) view, excluding the eyes (including the eyes when measured in males)
WL	Weber's length of the mesosoma (alitrunk): diagonal length, measured in lateral view, from the anterior margin of the pronotum (excluding the collar) to the posterior extremity of the metapleural lobe
PW	Pronotum width: maximum width of pronotum, measured in dorsal view
DPW	Dorsal petiolar width: maximum width of the petiolar node, measured in dorsal view
PH	Petiolar height: maximum measurable height of petiolar node, taken as a straight-line measurement in lateral view, from the summit of the node to the lowermost extremity of the subpetiolar process (Fig. 2)
PNL	Petiolar node length: length of the node, measured in lateral view, from the midpoints of maximum curvature where the anterior and posterior faces of the node meet the anterior and posterior peduncles, respectively (Fig. 2)

The following measurements were taken in a smaller series of workers ($n = 245$ for the first four measurements; $n = 40-60$ for the remainder) from all species:

- LF1 Length of first funicular segment: maximum length of the first funicular segment (pedicel), measured in dorsal view along its long axis and including the basal articulation
- LF2 Length of second funicular segment: maximum measurable length of second funicular segment, measured in dorsal view along its long axis
- SPL Length of subpetiolar process: length of the subpetiolar process from the ventral extremity to the uppermost part of the anterior margin, measured in lateral view along a line drawn from the ventral extremity to the anterodorsal margin of the anterior peduncle (Fig. 2)
- SPW Width of subpetiolar process: midlength width of the subpetiolar process, measured in lateral view at right angles to the length (Fig. 2)
- MFC Minimum frontal carinal distance: minimum distance between the frontal carinae, measured in full-face (dorsal) view, posterior to FCD (Fig. 1)
- EOL Distance between eye and occipital lobe: maximum measurable distance from the posterior margin of the compound eye to the posterior extremity of the occipital lobe, measured in oblique dorsolateral view
- IOD Inter-occipital lobe distance: distance between the posterior extremities of the occipital lobes, measured with the head capsule in posterodorsal view, between the points where the nuchal carina crosses the lobes
- LHT Length of hind tibia: length of the hind tibia, in dorsal view, including the basal constriction but excluding the condyle
- LHS Length of hind basitarsus: maximum measurable length of the hind basitarsus, in dorsal view

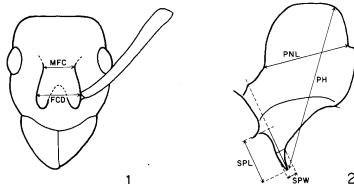


Fig. 1. Head of *Rhytidoponera* worker; frontal (full-face, dorsal) view, illustrating the measurement of maximum (FCD) and minimum (MFC) distances between the frontal carinae.

Fig. 2. Petiole of *Rhytidoponera* worker; lateral view, illustrating the measurement of petiolar height (PH), petiolar node (PNL), length of subpetiolar process (SPL), and width of subpetiolar process (SPW). SPW is taken at the mid-length of SPL.

Among the indices which were calculated from these measurements, the following are cited in the text:

- CI Cephalic index: HW/HL
- MI Mandibular index: ML/HW
- SI Scape index: SL/HW
- OI Ocular index: ED/HW
- FCI Frontal carinal index: FCD/HW
- PI Pronotal index: PW/HW
- PN12 Petiolar node width index, using HW: DPW/HW
- LPI Lateral petiolar index: PNL/PH
- DNI Dorsal petiolar node shape index: PNL/DPW
- FLI Funicular length index: LF2/LF1

SLI2	Index of subpetiolar process length, using HW: SPL/HW
SP1	Index of subpetiolar process width: SPW/SPL
FCC	Index of frontal carinal convergence: MFC/FCF
OLI	Occipital lobe index: EOL/HW
OLD	Index of occipital lobe distance: IOD/HW
HTI1	Hind tibial index: LHT/LHS
HTI2	Hind tibial index, using HW: LHT/HW

Since the foregoing ratios are conveniently scaled indices by themselves, the orthodox procedure of multiplying them by 100 was not followed.

In addition, three setal counts were made:

SSC	Scape setal count: the number of standing hairs, i.e. those forming an angle of 45° or more with the cuticular surface (Wilson 1955), visible in outline on the upper surface of the scape, with the line of view at right angles to the plane of funicular flexion
FSC	Fore femur setal count: the number of standing hairs visible in outline on the upper (extensor) surface of the fore femur, with the line of view at right angles to the plane of tibial flexion
HSC	Hind femur setal count: equivalent count for the hind femur

Apical tufts of setae were excluded in all setal counts.

Genetic and Ecological Information

Electrophoretic techniques used here were similar to those described in Ward (1980b), except that all loci, including esterase, were scored on 7% gels. The esterase locus reported here is probably homologous with the esterase-3 locus of Ward (1980b). Frozen material was stored at -70°C before electrophoresis. All species were examined electrophoretically except *wilsoni* Brown.

Ecological information is culled primarily from my field observations made during visits to New Caledonia in February–March 1977 and April–May 1980. A few nest-site and foraging records have been obtained from museum specimens (ANIC, MCZ).

Synopsis

Excepting *acanthoponeroides* Viehmeyer, the workers of New Caledonian species of *Rhytidoponera* can be distinguished from other members of the genus by possession of the following combination of features:

- (1) Occipital margin (i.e. posterior margin of the cranium, when head is seen in full-face (frontal) view) convex, flat, or weakly concave;
- (2) Occipital lobes slightly to moderately developed, not protruding extensively in lateral view (OLI 0.39–0.47, OLD 0.52–0.71);
- (3) Head a little longer than broad (CI 0.83–0.96);
- (4) Frontal lobes expanded laterally to cover most of the antennal insertions, the frontal carinae convex or straight, converging posteriorly (FCI 0.38–0.47, FCC 0.70–0.94);
- (5) Hind tibia relatively short, about the same length as the hind basitarsus (HTI1 0.93–1.07, HTI2 0.85–1.23).

These New Caledonian species most closely resemble some of the smaller *Rhytidoponera* species from eastern Australia. However, the latter possess one or more of the following features: (1) sinuous, medially indented, frontal carinae (e.g. *impressa* group, *croesus* Emery, *chnoopyx* Brown, *kurandensis* Brown), (2) well developed occipital lobes and a markedly concave occipital margin (e.g. *croesus*, *metallica* group), and/or (3) an elongate head (CI < 0.80) (*tenuis* group). The Australian species, *R. anceps* Emery, s.l., comes close to agreeing with the generalized diagnosis for the New Caledonian species of *Rhytidoponera*. The frontal carinae of *anceps* vary from weakly sinuous to a subparallel condition which approaches that found in some *pulchella* group species. The occipital margin of *anceps* is usually distinctly concave, and the occipital lobes appear to be a little better developed than those of any New

Caledonian species (OLI 0.45–0.49, OLD 0.69–0.75, in a sample of 10 workers from Western Australia, New South Wales, and Queensland).

Rhytidoponera acanthoponeroides does not agree with characteristics 2, 3, or 4 (the occipital lobes are conspicuously developed, the head is as wide as long, and the frontal carinae are parallel and upturned). It may be uniquely defined by the combination of the pointed petiolar node, parallel frontal carinae, and relatively short hind tibia (HT12 < 1.20).

Males are known for 10 of the 18 New Caledonian species of *Rhytidoponera*. No dealate females (queens) have been found, indicating the likelihood that the New Caledonian species have entirely worker-reproductive colonies [= type B colonies of Ward (1983)]. I have collected and dissected mated workers of most species (*aquila*, *arborea*, *atropurpurea*, *depilis*, *fulgens*, *koumensis*, *litoralis*, *luteipes*, *mimica*, *nitidiventris*, *numeensis*, *opaciventris*, and *versicolor*: see list below). With respect to external morphology, these mated workers differ in no substantial manner from their unmated nestmates.

Synonymic List of Species of New Caledonian Rhytidoponera

acanthoponeroides group

acanthoponeroides Viehmeyer, 1924

fulgens group

aquila, sp.nov.

atropurpurea Emery, 1914

fulgens (Emery, 1883)

= *socrula* Emery, 1914

opaciventris, sp.nov.

numeensis group

koumensis, sp.nov.

numeensis (André, 1889)

= *acupuncta* Emery, 1914

wilsoni Brown, 1958

pulchella group

arborea, sp.nov.

depilis, sp.nov.

insularis, sp.nov.

litoralis, sp.nov.

luteipes, sp.nov.

mimica, sp.nov.

nitidiventris, sp.nov.

pulchella (Emery, 1883)

terrestris, sp.nov.

versicolor, Brown 1958

Key to Species

Workers

1. *a* Larger species (HW > 1.40, WL > 2.30); either subpetiolar process very short (SL12 0.04–0.10) (e.g. Fig. 13), or petiolar node with a prominent posterodorsal point (Fig. 9); FLI > 0.80 2
- b* Smaller species (HW < 1.40, WL < 2.20); subpetiolar process well developed (SL12 0.11–0.21) (e.g. Figs 35, 47); dorsum of petiolar node not pointed; FLI < 0.80 6
- 2(1). *a* Subpetiolar process and dorsum of petiolar node both strongly pointed (Fig. 9) (SL12 0.18–0.20); head about as broad as long (CI 0.97–1.03) *acanthoponeroides* Viehmeyer

- b* Dorsum of petiolar node not pointed; subpetiolar process with a short, blunt tooth (e.g. Fig. 13) (SL12 0.04–0.10); head longer than broad (CI 0.84–0.94) 3
- 3(2). *a* Abdominal tergites III and IV densely shagreened, estriate except for the lateral margins (Fig. 12), the sculpture producing a matt appearance; remainder of body opaque, due to a fine, dense punctulation which covers the rugose sculpture; dark purplish black *atropurpurea* Emery
- b* Abdominal tergite IV (and usually also III) not notably shagreened, covered with variable amounts of fine, concentric, transverse striation (Figs 14, 22), opaque or shining; sculpture on remainder of body variable (striate to rugose, interspaces smooth or punctulate); body usually with greenish or purplish metallescent reflections 4
- 4(3). *a* Abdominal tergites III and IV shining, with predominantly transverse striation of variable density, often becoming weak medially, especially on the anterior margin of abdominal tergite IV (excluding the acrotergite) (Fig. 14); mesosoma predominantly rugostriate or striate, non-punctulate, and with strong greenish or green-purple iridescence; FSC often less than 10 (range 2–19) *fulgens* Emery
- b* Abdominal tergites III and IV opaque or subopaque, due to very dense, concentric, transverse striation which continues undiluted to the anterior margin of abdominal tergite IV (e.g. Fig. 24) and which may be obscured by punctulate sculpture on part of abdominal tergite III; mesosomal sculpture varying from rugose to striate, overlaid with variable amounts of punctulate sculpture (at least on the pronotum), the greenish or purplish iridescence correspondingly duller; FSC \geq 10 (range 10–19) 5
- 5(4). *a* Dorsum of mesosoma and of petiolar node rather densely and irregularly striate to rugostriate, nowhere distinctly rugose, even on the pronotum where weak inter-rugal punctures are obscured by denser striate sculpture (and overlaid by weak punctulation); black, with relatively weak violaceous reflections *aquila*, sp. nov.
- b* Dorsal surface of pronotum rugose, variably overlaid with fine punctulation, but with inter-rugal punctures generally large and distinct; remainder of mesosomal dorsum varying from rugostriate to rugose; greenish or purplish iridescence usually conspicuous *opaciventris*, sp. nov.
- 6(1). *a* Petiolar node strongly compressed in lateral view (Fig. 33) (LPI 0.32–0.35; DNI 0.53–0.60); subpetiolar process consisting of a broad keel with a short spiniform point *wilsoni* Brown
- b* Petiolar node not strongly compressed (LPI 0.43–0.59; DNI 0.61–1.01); subpetiolar process not as above 7
- 7(6). *a* Subpetiolar process consisting of a broad triangular or subrectangular keel, without a spiniform point (Figs 35, 37) (SPI 0.44–1.23); mesosoma robust (Fig. 30), with a broad pronotum (PI 0.79–0.88) 8
- b* Subpetiolar process consisting of a slender spiniform point (e.g. Figs 47, 49) (SPI 0.10–0.31); mesosoma relatively slender (e.g. Fig. 42) (PI 0.72–0.83) 9
- 8(7). *a* Larger species (HW \geq 1.23); posterior margin of subpetiolar process concave, sinuous, or angled inward in lateral view (Fig. 37) (SPI 0.44–0.87) ... *koumientsis*, sp. nov.
- b* Smaller species (HW \leq 1.23); posterior margin of subpetiolar process usually convex or angled outward in lateral view (Fig. 35) (SPI 0.91–1.23) *numeensis* André
- 9(7). *a* Abdominal tergites III and IV smooth and strongly shining, with few or no appressed hairs, and generally devoid of sculpture except for weak anterolateral striae (Fig. 26); body dorsum covered with numerous erect and suberect hairs, the longest of which are considerably greater than the eye diameter *versicolor* Brown
- b* Abdominal tergites III and IV opaque or shining, appressed and decumbent hairs always present, usually common to abundant (erect pilosity also present), and sculpture varying from rugostriate to weakly striolate, seldom completely effaced, at least on abdominal tergite III; if abdominal tergite III is more or less smooth and shiny, then the appressed gastric hairs are conspicuous, and/or the longest erect setae of the body dorsum \leq the eye diameter 10

- 10(9). a Head, mesosoma, and petiole dark brown to black, with strongly contrasting, pale luteous legs, mandibles, and antennae; petiole with a relatively long anterior peduncle and short subpetiolar process (DNI 0.73–0.86; SL12 0.12–0.16) (Fig. 57); SSC 3–15 *luteipes*, sp. nov.
- b Body varying from light ferruginous brown to dark brown or black, appendages usually a lighter brown and showing no more than a modest contrast with the body; if the appendages are pale luteous and contrast markedly with a black mesosoma, then the head and gaster are also light and contrasting, and SSC 0–1; petiole shape variable 11
- 11(10). a Abdominal tergite IV opaque to sublucid, covered with a dense mat of fine appressed pubescence which partly obscures the underlying striolate-imbricate sculpture (e.g. Figs 50, 60) 12
- b Abdominal tergite IV at least partly shining, weakly striate or smooth; appressed hairs coarser and much less dense, separated by about their lengths (e.g. Figs 70, 74) 16
- 12(11). a Larger species (HW 1.00–1.32; WL 1.54–2.00); petiolar node robust, with short anterior peduncle (e.g. Fig. 49) (LPI 0.49–0.59) 13
- b Smaller species (HW 0.80–0.96; WL 1.19–1.42); petiolar node tending to be more slender (e.g. Fig. 61) (LPI 0.45–0.54) 15
- 13(12). a Erect pilosity very sparse or absent on the dorsum of head, mesosoma, and petiole, completely lacking on the scapes and legs; gastric tergites densely covered with appressed, multi-branched pubescence (Fig. 46) *depilis*, sp. nov.
- b Erect pilosity common on the upper surface of the body, and present on the scapes and legs; gastric pubescence less dense and most hairs unbranched 14
- 14(13). a Scapes and upper surface of femora with numerous erect setae (SSC 10–18; FSC 1–15; HSC 8–19); occipital lobes broadly rounded and protruding only slightly in lateral view (OLI 0.40–0.44; OLD 0.66–0.71) *terrestris*, sp. nov.
- b Scapes and upper surface of femora with fewer erect setae (SSC 7–10; FSC 0–2; HSC 0–6; occipital lobes more narrowly rounded (OLI 0.43–0.46; OLD 0.62–0.66) *arborea*, sp. nov.
- 15(12). a Fine, erect pilosity abundant on upper surface of body (Fig. 56); in lateral view, > 20 standing hairs visible in outline on mesosoma dorsum; SSC 2–14; entire body dark brown to black (appendages lighter) *pulchella* Emery
- b Erect pilosity rather sparse on upper surface of body (Fig. 54); < 12 standing hairs visible in outline on mesosoma dorsum; SSC 0–2; gaster testaceous brown, conspicuously lighter than the dark brown head and mesosoma *insularis*, sp. nov.
- 16(11). a Smaller species (HW 0.86–0.92; WL 1.22–1.34); mesosoma and petiole dark brown to black, with contrasting ferruginous brown head and luteous gaster and appendages; scapes and femora with few standing hairs (SSC 0–1, FSC 0) *mimica*, sp. nov.
- b Larger species (HW 0.95–1.14; WL 1.37–1.65); body unicolorous, varying from light ferruginous brown to black; pilosity on scapes and femora variable 17
- 17(16). a Abdominal tergite III opaque, covered with dense, transverse striation and conspicuous, elongate punctures; erect pilosity sparse on scapes and femora (SSC 0–2, FSC 0); body dark brown to black *nitidiventris*, sp. nov.
- b Abdominal tergite III shining, weakly striolate, and without conspicuous elongate punctures; erect pilosity common on scapes and femora (SSC 4–21, FSC 0–10); body varying from light ferruginous brown to dark brown *litoralis*, sp. nov.

Males

Males are known for *Rhytidoponera acanthoponeroides*, all of the *fulgens*-group species, two of the three *numeensis*-group species (unknown in *wilsoni*), and three of the ten species in the *pulchella* group. Therefore, no attempt has been made to key males down to species in the last-named group.

1. a Larger species (HW, including eyes, > 1.45); eyes densely hairy (*fulgens* group) .. 2
- b Smaller species (HW, including eyes, < 1.40); eyes not hairy 5
- 2(1). a Erect pilosity on antennal scapes rather sparse (SSC 1–6); scapes relatively short (SI 0.40–0.50); abdominal tergites III and IV smooth and shining, more or less devoid of sculpture, except for scattered small punctures and very faint (obsolete) striation *fulgens* Emery

- b* Erect pilosity moderately dense on scapes (SSC 7–16); scapes longer (SI 0.48–0.62); abdominal tergites III and IV sublucid to shining, usually partly covered with weak striation, dense punctures, or both 3
- 3(2). *a* Mesonotum longitudinally rugostriate, the interspaces punctulate; abdominal tergites III and IV with faint transverse striation becoming finely reticulate towards the posterior margins *atropurpurea* Emery
- b* Mesonotum strigulate to rugostriate, at least some interspaces shining and without conspicuous punctulate sculpture; sculpture on abdominal tergites III and IV variable, but usually not distinctly microreticulate 4
- 4(3). *a* Abdominal tergites III and IV with faint and partially obsolete striae, oriented predominantly longitudinally; abdominal tergite IV with elongate punctures, which in the region of greatest density (median area) are separated by no more than their lengths *aquila*, sp.nov.
- b* Abdominal tergites III and IV with faint, transversely oriented striae; abdominal tergite IV with scattered punctures, of variable density *opaciventris*, sp.nov.
- 5(1). *a* Antennal scape long, equal to or exceeding the length of the 1st 4 funicular segments (SI 0.75–0.91) (*numeensis* group) 6
- b* Antennal scape much shorter, less than or equal to the length of the 1st 2 funicular segments (SI 0.21–0.30) 7
- 6(5). *a* Median carina (on frons) weakly developed, and scarcely distinct from adjacent striae sculpture; larger species, with relatively long scapes (HW 1.19, SL 1.08, SI 0.91, in single male examined) *koumensis*, sp.nov.
- b* Frons with well developed median carina; smaller species, with slightly shorter scapes (HW 1.09–1.19, SL 0.88–0.98, SI 0.75–0.83, in a sample of 8) *numeensis* André
- 7(5). *a* Antennal scape $\approx \frac{1}{2}$ length of 2nd funicular segment; subpetiolar process lacking *acanthoponeroides* Viehmeyer
- b* Antennal scape \approx length of 2nd funicular segment; subpetiolar process present as a distinct spiniform tooth *pulchella* group*

*Based on males of *terrestris* sp.nov., *luteipes* sp.nov., and *versicolor* Brown.

Species Descriptions

The *acanthoponeroides* group

Rhytidoponera acanthoponeroides Viehmeyer

(Figs 3, 4, 9, 10)

Rhytidoponera acanthoponeroides Viehmeyer, 1924, p. 227. Holotype worker, New Caledonia, not in MNHU.

Rhytidoponera acanthoponeroides Viehmeyer, Brown, 1958, p. 289 [description of male].

Worker measurements. HW 1.52–1.80, WL 2.35–2.82, CI 0.97–1.03, MI 0.34–0.41, SI 0.97–1.10 ($n=19$); SLI2 0.18–0.20, SSC 8–21, FSC 2–4 ($n=10$).

Diagnosis of Worker

Anterior clypeal margin convex, median clypeal area carinate. Frontal carinae parallel and upturned, c. $\frac{1}{5}$ – $\frac{1}{2}$ of the antennal insertions exposed in full-face (dorsal) view; FCI 0.35–0.39. Head quadrate, as broad as long, its sides weakly convex, occipital margin flat to weakly convex. Eyes relatively small (OI 0.17–0.21), protruding slightly in dorsal view. In lateral view, vertex forms a distinct obtuse angle (c. 120°) with median area of frons, and occipital lobes protrude distinctly. Promesonotal suture distinctly impressed, evenly rounded in dorsal view. Mesonotum and propodeum more or less evenly convex in lateral view, the basal and declivitous faces of the propodeum not differentiated. Inferior pronotal tooth distinct and protruding. Petiole as illustrated, with robust, mucronate node (LPI

0.40–0.49; DNI 0.86–1.02) and spine-like subpetiolar process (SLI2 0.18–0.20; SPI 0.14–0.37).

Mandibles striate. Head longitudinally carinate. Pronotum typically rugose, with median area showing weak longitudinal orientation of the rugae, contrasting with remainder of the mesosoma which is transversely carinate or strigate. Dorsum of petiolar node rugose, rugae becoming increasingly parallel and regular on sides and anterior face of node. Gaster smooth with faint, scattered punctures, and varying from subopaque to shining. Most parts of the body (although not upper surface of fore femur) covered with fine, flexuous hairs. Body a metallescent purplish green, with contrasting ferrugineous legs, mandibles, and antennae.

Comments

R. acanthoponeroides was described by Viehmeyer (1924) on the basis of a single worker received from Emery. The type could not be located in MNHU (F. Koch, personal communication), but the original description leaves little doubt about the identity of this species. Moreover, in the MCSN there is a single worker from Ngoyé (19 September 1911) labelled 'n.sp.' in Emery's handwriting. Three other Ngoyé workers, evidently part of the same series, are in NHMB. This Ngoyé material agrees well with the original description, and it seems likely that the specimen which Viehmeyer received from Emery also came from this series.

R. acanthoponeroides can be recognized by the mucronate petiolar node, distinctive body sculpture, head shape, and fine flexuous hairs. There is notable variation in colour, body sculpture, and lustre. Workers from northern and western populations (Mt Rembai, Table Unio, Coula-Boréaré, Col des Roussettes, Mt Aoupinié) tend to be shinier, with the pronotum predominantly transversely rugostriate to carinate, and the appendages darker brown (contrasting less with the rest of the body). Further collections from intermediate localities are necessary to determine whether these northern populations represent a distinct species. The kind of differentiation seen is not unexpected for populations occupying isolated montane 'islands'.

Ecology

From present records, this species appears to be restricted to rainforest and cloud forest at higher elevations (500–940 m). At Montagne des Sources a worker was collected foraging in open heath or maquis [this habitat is illustrated by Holloway (1979, p. 59)], about 20 m from the nearest gully with tall woody shrubs; all other records, including other ground foragers from Montagne des Sources, are from closed forest. Collections come from both sedimentary and ultramafic localities. Nest-site records: under stone (1); in clump of soil and rotting wood (1).

Material Examined

Montagne des Sources, 780 m; Mt Koghis, 650 m, 800 m; Mt Koghis, 750 m; Ngoyé; Mt Mou; Mt Rembai, 800 m; Table Unio, 680–725 m; Col des Roussettes, nr Bourail, 500–600 m; Coula-Boréaré; Mt Aoupinié, 940 m. In ANIC, BMNH, MCSN, MCZ, NHMB, PSW.

The *fulgens* group

Rhytidoponera aquila, sp.nov.

(Figs 15, 16, 21, 22)

Type Material

Holotype worker. New Caledonia: 3 km SW. Touho, 400 m, 20°48'S., 165°13'E., 20.iv.1980, nest in soil, rainforest (P. S. Ward acc. No. 4074) (ANIC Type No. 7579).

Paratype workers, males. A series of 3 accessions from 3 km SW. Touho, 270–400 m (P. S. Ward acc. Nos 4067, 4074, 4078) (ANIC, BPBM, BMNH, MNHN, PSW).

Measurements

Holotype worker. HW 1.54, WL 2.61, CI 0.87, MI 0.35, SI 1.20, SLI2 0.07, SSC 17, FSC 15.

Paratype workers. HW 1.45–1.58, WL 2.50–2.68, CI 0.84–0.88, MI 0.32–0.37, SI 1.17–1.24 ($n=13$); SLI2 0.06–0.08, SSC 15–20, FSC 12–19 ($n=9$).

Diagnosis of Worker

Anterior clypeal margin convex to weakly angulate. Frontal lobes expanded laterally to cover most of the antennal insertions. Frontal carinae convex and converging posteriorly to $c. \frac{3}{4}$ their maximum distance; the latter (FCD) $c. \frac{2}{3}$ of the head width (FCI 0.41–0.43). Head quadrate, longer than wide, the sides weakly convex, occipital margin weakly convex or flat. Eyes protruding slightly in dorsal view, OI 0.23–0.27. In lateral view, the median area of the frons rounds evenly into the vertex, and the occipital lobes are broadly rounded and non-protruding. Pronotum relatively slender, PI 0.74–0.79. Promesonotal suture distinct, evenly rounded in dorsal view. Mesopropodeal impression very weak, scarcely evident in lateral view; basal and declivitous faces of the propodeum weakly differentiated. Inferior pronotal tooth distinct. Petiolar node as illustrated: robust (DNI 0.90–1.03), subrectangular, with a short anterior peduncle and poorly developed subpetiolar process (SLI2 0.06–0.08).

Mandibles densely striate. Head longitudinally rugostriate, a fine striation overlying the coarse longitudinal rugae, inter-rugal punctures indistinct. Pronotum with obsolete rugae, overlaid by dense and weakly punctulate striation, showing a predominant longitudinal orientation, at least on the posteromedial area of the pronotum. Remainder of mesosoma and petiolar node transversely striate to finely rugostriate. Abdominal tergites III and IV with dense, concentric, transverse striation and with weak, scattered punctures. On abdominal tergite IV the striae are concentric around a point located variably on the posterior half of the tergite, so that in dorsal view the posterior third of abdominal tergite IV is often longitudinally striate. Fine, erect setae common on most parts of body. Body violaceous-black, with finely scattered iridescence. Legs, mandibles, and antennae dark brown, the legs and antennae lighter apically.

Comments

Known only from the rainforest-covered hills near Touho, *aquila* appears to be related to the complex of *opaciventris* populations farther west, on the basis of the densely striate, opaque gaster. *R. aquila* is given species status because of the distinctive striate sculpture which covers most of the head and mesosoma (*opaciventris* tends towards more rugose sculpture, at least on the pronotum) and because the Touho population is substituted for a unique superoxide dismutase (*SOD-1*) allele found in no other *fulgens*-group species. It would be of interest to examine the status of populations in intermediate localities, particularly rainforest areas immediately north-west and south-east of the Tipindje River.

Ecology

Workers were seen foraging on the ground and on low vegetation, in rainforest between 270 and 400 m. Nest-site records: directly in the soil (1).

Rhytidoponera atropurpurea Emery

(Figs 5, 6, 11, 12)

Rhytidoponera atropurpurea Emery, 1914, p. 396. Syntype workers, males, New Caledonia: Hienghène, June 1911 (Sarasin and Roux) (MCSN, MCZ, MHN, NHMB) [examined]. A single syntype worker in MCZ here selected as **lectotype**.

Rhytidoponera atropurpurea Emery; Brown, 1958, p. 292.

Worker measurements. HW 1.64–1.85, WL 2.68–2.95, CI 0.87–0.94, MI 0.27–0.38, SI 1.07–1.17 ($n = 19$); SL12 0.06–0.09, SSC 13–20, FSC 9–17 ($n = 10$).

Diagnosis of Worker

Similar in relative body dimensions and habitus to *aquila* (q.v.) and other *fulgens*-group species, although averaging larger (HW 1.64–1.85). Differing from these other species principally in details of body sculpture.

Mandibles densely striate. Head predominantly rugose (becoming rugostriate on the genae and underside of head), overlaid by conspicuous punctulate sculpture which gives an opaque texture. A similar pattern seen on the mesosoma and petiolar node, where the punctulation is even denser and the rugose sculpture even more obscured. Abdominal tergites III and IV with a matt texture, due to very dense shagreening, all striation obliterated except on the lateral margins. Abdominal sternites III and IV subopaque with weak, reticulo-striate, non-punctulate sculpture, and a smooth, shiny area devoid of sculpture (except for scattered punctures) on the posteromedial part of abdominal sternite III. Fine erect setae common on most parts of the body. Dull black, with glinting violaceous reflections; mandibles dark brown; antennae and legs dark brown, lighter apically.

Comments

R. atropurpurea is distinguished from other *fulgens*-group species by the densely punctulate sculpture, which imparts a matt appearance to the body. This is particularly noticeable on the gastric tergites which are densely shagreened and devoid of transverse striation. Some *opaciventris* populations (vicinity of Hienghène) have workers in which the density of punctulation on the head and mesosoma approaches that of *atropurpurea*, but in these specimens the rugae on the head show a more distinct longitudinal orientation and abdominal tergite IV is transversely striate.

Ecology

This species has been collected in rainforest from 40 to 520 m elevation. Workers were seen foraging on the ground and on vegetation. Nest-site records: directly in soil (2); ex rotten log (4); in cavity in standing tree (2). Apart from the two arboreal nest-site records (from living trees), two of the rotting log records refer to nests in recently fallen tree trunks in early stages of decay.

Material Examined

Aoupinié For. Reserve, 460 m, 520 m; Ste Thérèse, Amoa R, 40 m; I Ouedjo [= Ouendjo?], Hienghène [*atropurpurea* lectotype and paralectotypes]: 8 km ESE Tieta, 100 m. In ANIC, BPBM, BMNH, MCSN, MCZ, MHN, MNHN, NHMB, PSW.

Rhytidoponera fulgens (Emery)

(Figs 7, 8, 13, 14)

Ectatomma fulgens Emery, 1883, p. 148. Holotype worker, New Caledonia (MCSN) [examined].

Rhytidoponera (*Chalcopyonera*) *fulgens* (Emery); Emery, 1914, p. 395.

Rhytidoponera (*Chalcoponera*) *fulgens* var. *socrula* Emery, 1914, p. 395. Syntype workers, New Caledonia [Coulas-Boréaré] (Sarasin and Roux) (MCSN, MHN, NHMB) [examined] [synonymy by Brown, 1958, p. 203].

Rhytidoponera fulgens (Emery); Brown, 1958, p. 286.

Rhytidoponera fulgens (Emery); Ward, 1981, p. 111.

Worker measurements. HW 1.42–1.72, WL 2.39–3.10, CI 0.84–0.91, MI 0.32–0.43, SI 1.13–1.28 ($n=97$); SLI2 0.04–0.10, SSC 10–19, FSC 2–19. ($n=24$).

Diagnosis of Worker

Agreeing with *aquila* (q.v.) and other *fulgens*-group species in relative body dimensions and shape. Petiolar node averaging a little shorter (LPI 0.52–0.62).

Mandibles densely striate. Head longitudinally rugostriate, the rugae diverging from midline on the frons and vertex, and oriented concentrically around the eyes and (to a varying degree) around the antennal fossae. Interspaces between rugae shining. Pronotum varying from rugose to rugostriate; remainder of mesosoma and petiolar node predominantly transversely rugostriate, the interspaces shining. Abdominal tergites III and IV shining, with small, scattered punctures and with (variably developed) fine, usually transverse, striation, which is never sufficiently strong to dull the lustre on the tergites. Fine, erect setae scattered over most of body, averaging a little less dense than in other *fulgens*-group species (median SSC 14, median FSC 8). Dark black-brown, with rather conspicuous greenish or purplish metallescent reflections. Legs, mandibles, and antennae dark brown.

Comments

R. fulgens differs from other *fulgens*-group species by the shinier gastric tergites and by the absence of punctulate sculpture. The rugae on the head often show a concentric orientation around the antennal fossae. The erect setae also tend to be less dense on *fulgens* workers. Within these constraints, *fulgens* varies considerably in body sculpture and pilosity. The pronotum may be rugose without definite orientation of the rugae, transversely striate to rugostriate (as in the holotype), or predominantly longitudinally rugostriate. The fine, transverse striation on abdominal tergites III and IV varies from moderately dense (though never dulling the lustre of the tergites to the same degree as in *aquila* or *opaciventris*) to almost obsolete; the holotype is intermediate in this regard. In most populations the fore-femur setal count (FSC) is rather low (0–11 in a sample of 87 workers from 20 localities; 5 in the holotype); but the *fulgens* population in the Aoupinié Forestry Reserve is exceptional in having more setose femora (FSC 7–19 in a sample of 15 workers).

The range of *fulgens* overlaps that of *atropurpurea*, and the two species remain quite distinct from one another. However, *fulgens* has not been collected sympatrically with *opaciventris* or *aquila*, and, given the amount of variation shown by both these species, it is possible that forms morphologically intermediate between *fulgens* and *aquila* will be found in rainforest areas between Touho and Aoupinié.

Ecology

R. fulgens occurs in rainforest across a considerable range of elevation (40–900 m), although it appears to be uncommon in high-altitude moss forest. Workers forage both on the ground and on low vegetation. Nests occur directly in the soil (5 records), under stones (4), and in rotting logs (8).

Material Examined

N. Caléd. [*fulgens* holotype]; St Louis; St Louis Mission, 120 m; Mt Koghis, 350 m, 450 m, 500 m, 600 m, 650 m; Monts Koghis, Auberge, 500 m; Chapeau Gendarme, Yahoué; Yahoe, 12 km N.

Nouméa; 8 km N. Dumbéa, 650 m; Mt Mou, 180 m, 400–800 m; Col de la Pirogue; Bouloupari to Thio, km 10, 270 m; Bouloupari to Thio, km 7, 100 m; Mt Do, 750 m; Ciu, nr Mt Canala, 300 m; Mt Canala, 700 m; Negropo; La Crouen, 130 m; Sarraméa, 160 m; Koh; La Foa; Col d'Amieu, Mé Onguè, 700 m; Col d'Amieu; Col d'Amieu Stn, 360 m, 440 m; Toili R, Col d'Amieu For. Stn, 350 m; Toma R, Col d'Amieu For. Stn, 380 m; Table Unio, 680 m, 725 m, 800 m; Col de Hô, 40 m; 'Col de Hau'; Col des Roussettes, 500–600 m, 400 m, 550 m; Coula-Boréaré [*socrula* syntypes]; 2 km SE. Bogui, 170 m; Aoupinié For. Reserve, 460 m, 520 m; Mt Aoupinié, 825 m, 900 m; Koné. In ANIC, BPBM, BMNH, MCSN, MCZ, MHN, NHMB, PSW.

***Rhytidoponera opaciventris*, sp. nov.**

(Figs 17, 18, 23, 24)

Rhytidoponera numeensis; Emery (nec André), 1914, p. 395 (partim).

Type Material

Holotype worker. New Caledonia: Mt Panié, 100 m, 20°34'S., 164°46'E., 23.iv.1980, under stone in rainforest (P. S. Ward acc. No. 4094) (ANIC Type No. 7588).

Paratype workers, males. (1) A series of 14 accessions from Mt Panié, 100 m, 300 m, 360 m, 390 m, 520 m, 600 m, 750 m (P. S. Ward acc. Nos 2172, 2184–1, 2185, 2189, 2190, 2200, 2205, 2208, 2213, 2214–1, 2215, 4081, 4082, and 4094) (ANIC, BPBM, BMNH, MCZ, MNHN, and PSW). (2) Mt Panié, 350 m, 28.x.1978 (J. C. Watt), 3 workers (ANIC). (3) Mt Panié, 500 m, 27.vi.1911 (Sarasin and Roux), 1 worker (NHMB).

Non-paratypic material. Additional material which is considered to be conspecific is listed below (under *Material Examined*).

Measurements

Holotype worker. HW 1.62, WL 2.60, CI 0.91, MI 0.35, SI 1.13, SLI2 0.09, SSC 20, FSC 14.

Paratype workers and other material. HW 1.44–1.71, WL 2.36–2.85, CI 0.85–0.93, MI 0.30–0.40, SI 1.04–1.22 ($n=78$); SLI2 0.05–0.09, SSC 14–24, FSC 10–18 ($n=23$).

Diagnosis of Worker (type material only)

Agreeing with *aquila* (q.v.) and other *fulgens*-group species in relative body dimensions and shape.

Mandibles densely striate. Head longitudinally rugostriate, the rugae diverging posteriorly and becoming irregular on the vertex, where there are distinct inter-rugal punctures; interspaces shining. Rugae or striae arranged concentrically around the posterior half of the eyes, but not around the antennal fossae. Pronotum rugose, the rugae without a strong directional orientation, but overlaid by weak striate and punctulate sculpture. Remainder of mesosoma and petiolar node predominantly transversely rugostriate, with both large inter-rugal punctures and fine punctulation rather weak and scattered. Abdominal tergites III and IV subopaque to opaque, with fine, dense, concentric, transverse striation, and with scattered, elongate punctures which are more conspicuous on abdominal tergite III than IV. Fine, erect setae common on most parts of the body. Black-brown with violaceous and greenish reflections; legs, mandibles, and antennae dark brown.

Comments

This species may be characterized by the opaque, densely striate gastric tergites, and by the rugose pronotum which is variably overlaid with punctulate sculpture. At the type locality, the sculpture on the remainder of the mesosoma and on the head is predominantly rugostriate, with little overlying punctulation. Elsewhere on the Panié massif, and also in the

vicinities of Hienghène and Koumac, are populations which I am considering conspecific with *opaciventris*. The workers in these populations have more rugose sculpture on the head and mesosoma, and the latter is densely punctulate. These populations also show divergent colour patterns: the workers from near Hienghène are black with dull, violaceous reflections; while those from northwest of Mt Panié (Mt Ignambi, Col d'Amoss, Col d'Amoss) and from the vicinity of Koumac tend to have light ferruginous-brown legs which contrast with the darker, greenish purple, iridescent body. The Grottes de Koum population (but not that from Col d'Amoss) is also fixed for a unique phosphoglucosylase (*PGM*) allele.

Whether these variably differentiated, allopatric populations should be given specific status is largely an arbitrary judgment. For the time being it seems more convenient to refer to them as sets of geographically delimited populations of a single species.

Ecology

Records come from wet lowland rainforest, dry rainforest on limestone, gully rainforest, and montane rainforest, over an altitudinal range of 40 to 750 m. Workers have been seen foraging on the ground and on low vegetation. Nest-site records: under stone (8); ex rotten log (8).

Material Examined

(1) Vicinity of Hienghène: 9 km SW. Hienghène, 40 m, 140 m; Roches d'Ouaième, 750 m. (2) Panié massif: Mt Panié, 100–750 m [type material]; Mt Ignambi, 700 m; Col d'Amoss, 300 m. (3) Koumac region: Tchalebel, 7 miles E. Koumac; Grottes de Koum, 40 m; 9 km NNE. Koumac, 80 m. In ANIC, BPBM, BMNH, MCSN, MCZ, MHN, MNHN, NHMB, PSW.

The *numeensis* group

Rhytidoponera koumensis, sp. nov.

(Figs 31, 32, 37, 38)

Rhytidoponera numeensis; Emery (nec André), 1914, p. 395 (partim).

Type Material

Holotype worker. New Caledonia: Grottes de Koum, 40 m, 20°32'S., 164°20'E., 3.v.1980, nest in soil, dry rainforest on limestone (P. S. Ward, acc. No. 4209) (ANIC Type No. 7583).

Paratype workers, one male: (1) A series of 3 accessions from Grottes de Koum, (P. S. Ward acc. Nos 4196, 4202, 4209) (ANIC, BPBM, BMNH, MCZ, MNHN, PSW). (2) A series of 7 workers from 9 km NNE. Koumac, 80 m, 20°29'S., 164°18'E., 3.v.1980, foraging on ground, rainforest (P. S. Ward acc. No. 4210) (ANIC, PSW).

Non-paratype material: Tchalebel, 5.v.1911 (Sarsin and Roux), 1 worker (MCSN). This worker is on a pin with an *opaciventris* worker and male.

Measurements

Holotype worker. HW 1.31, WL 2.01, CI 0.92, MI 0.33, SI 0.97, SLI2 0.13, SSC 15, FSC 11.

Paratype workers. HW 1.23–1.39, WL 1.92–2.12, CI 0.89–0.94, MI 0.28–0.33, SI 0.93–1.01 ($n=16$); SLI2 0.12–0.13, SSC 13–18, FSC 8–16 ($n=9$).

Diagnosis of Worker

Anterior clypeal margin convex to weakly angulate. Frontal lobes expanded laterally and covering most of the antennal insertions; frontal carinae weakly convex, converging posteriorly to c. 85% of their maximum distance; the latter (FCD) a little more than $\frac{2}{3}$ of the head width (FCI 0.41–0.46). Head quadrate, longer than wide, the sides weakly convex, the

occipital margin flat. Eyes protruding slightly in dorsal view, OI 0.20–0.23. In lateral view, the median area of the frons rounds rather narrowly into the flattened vertex; the occipital lobes broadly rounded and inconspicuous. Mesosoma rather robust, with a relatively broad pronotum (PI 0.80–0.85). Promesonotal suture distinct, evenly rounded in dorsal view. Mesopropodeal impression indistinct; basal face of propodeum rather short, weakly differentiated from the long declivitous face which is flat to slightly concave in lateral view. Inferior pronotal tooth well developed. Petiole as illustrated: the node higher and wider than long (LPI 0.45–0.52; DNI 0.68–0.82). Subpetiolar process moderately well developed (SLI2 0.12–0.13), consisting of a broad tooth (SPI 0.44–0.86), with a variably sinuous or concave posterior margin.

Mandibles densely striate. Head longitudinally rugostriate, with scattered, coarse punctures towards the vertex; overlaid by fine, irregular striate sculpture. Mesosoma and petiolar node predominantly rugose, becoming rugostriate laterally, and overlaid with weak, punctulate-striolate sculpture. Abdominal tergites III and IV opaque, with weak, obsolete punctures and with fine, concentric, transverse striation, becoming arched-transverse and longitudinal on their posterior halves. Fine, erect setae common on most parts of body. Dark brown with glinting reflections; mandibles, antennae, and legs a little lighter, not strongly contrasting.

Comments

The robust mesosoma, dark brown color, and broad subpetiolar process place *koumensis* in the *numeensis* group. It differs from *wilsoni* in size, shape of the petiolar node, shape of the subpetiolar process, sculptural details, and pilosity (SSC > 12 in *koumensis*, SSC < 12 in *wilsoni*). *R. koumensis* and *numeensis* are quite close, and are distinguishable primarily by the differences outlined in the key. The posterior margin of the subpetiolar process is sinuous, concave, or angled inward in *koumensis* (usually convex or angled outward in *numeensis*), so that the subpetiolar process is more slender than that of *numeensis* and the SPI values do not overlap. In addition, *koumensis* is larger and has a more setose fore femur (FSC 8–16 in *koumensis*, 0–9 in *numeensis*).

Ecology

The type material was collected in rather dry rainforest on limestone (see Holloway (1979, p. 120) for an illustration of the habitat at Grottes de Koum), where workers were observed foraging on the ground. Nest-site records: directly in soil (2).

Rhytidoponera numeensis (André)

(Figs 29, 30, 35, 36)

Ectatomma (*Rhytidoponera*) *numeense* André, 1889, p. 221. Two syntype workers, New Caledonia: Nouméa (MNHN) [examined]. One syntype here selected as **lectotype**.

Rhytidoponera (*Chalcoponera*) *acupuncta* Emery, 1914, p. 396. Syntype workers, males, New Caledonia: Yaté, 24.iii.1912 (Sarsin and Roux) (MCSN, MHN, NHMB) [examined] [synonymy by Brown, 1958, p. 204].

Rhytidoponera pulchella; Emery (nec Emery, 1883) 1914, p. 396 (partim).

Rhytidoponera numeensis (André); Brown, 1958, p. 291.

Worker measurements. HW 1.02–1.23, WL 1.58–1.94, CI 0.85–0.92, MI 0.30–0.37, SI 0.95–1.07 ($n=83$); SLI2 0.11–0.14, SSC 12–18, FSC 0–9 ($n=20$).

Diagnosis of Worker

Agreeing with *koumensis* (q.v.) in relative body dimensions and sculpture, except smaller. Declivitous face of propodeum more notably concave in lateral view. Posterior

margin of subpetiolar process usually convex or angled outward. Elongate punctures more distinctly impressed on abdominal tergites III and IV. Fine, erect setae common on most parts of the body. Dark brown, with glinting reflections; mandibles, antennae, and legs lighter brown, often contrasting somewhat with the body.

Comments

Differences between *koumensis* and *numeensis* have been discussed under the former species. *R. numeensis* differs from *wilsoni* in having less pronounced occipital lobes, a longer petiolar node (LPI 0.43–0.52 in *numeensis*, 0.32–0.35 in *wilsoni*), and a shorter, broader subpetiolar process without a spiniform point (SLI2 0.11–0.14 in *numeensis*, 0.16–0.21 in *wilsoni*). In addition, the rugose sculpture of the head and mesosoma of *numeensis* is more obscured by overlying punctulate-striolate sculpture than in *wilsoni*.

R. numeensis shows considerable variation in the shape of the subpetiolar process (note the range of SPI values: 0.91–1.23) and in some details of sculpture. The dense striation on abdominal tergite IV varies from entirely longitudinal to (more typically) concentrically transverse on the anterior half, becoming arched-transverse or longitudinal on the posterior half of the tergite.

Ecology

The most widely distributed of all New Caledonian *Rhytidoponera*, *numeensis* occurs in littoral forest and upland rainforest, from sea level to 750 m. Workers forage almost exclusively on the ground (i.e. not on low vegetation). Nest-site records: directly in soil (2), under stone (7), ex rotten log (6).

Material Examined

Baie d'Oupî, Ile des Pins, < 5 m; Kuto Peninsula, Ile des Pins, 5 m; Ouro, Ile des Pins, 5 m; 3 km N. Goro, 5 m; 6 km SE. Touaourou, < 5 m; Fausse Yaté R., 10 m; Yaté [*acupuncta* syntypes]; Mt Ouénarou, 300 m; Col de Mourange, 300 m, 240 m; Rivière Bleue, 170 m; la Coulée R., 8 km NE. St Louis, 100 m; Montagne des Sources, 560 m; St Louis Mission, 120 m; Thi Rivière, 120 m; Koghis Cascade, 650 m; Mt Koghis, 450 m, 500 m, 750 m; Monts Koghis, Auberge, 500 m; Chapeau Gendarme (Yahoué), Yahoué, 12 km N. Nouméa; Nouméa [*numeensis* lectotype and paralectotype]; 8 km N. Dumbéa, 650 m; Mt Mou, 180 m; Kuenthio R., 14 km SW. Thio, 40 m; Bouloupari to Thio, km 10, 270 m; Ciu, nr Mt Canala, 300 m; La Crouen, 130 m; Sarraméa, 160 m; Koh; Col d'Amieu Stn, 360 m; Toma R., Col d'Amieu For. Stn, 380 m; Col de Hô, 40 m; 'Col de Hau', 2 km SE. Bogui, 170 m; 2 km W. Touho, < 5 m; Thiem R., 22 km ESE. Hienghène; Hienghène; 9 km SW. Hienghène, 40 m, 140 m; Oubatché, 40 m. In ANIC, BMNH, MCSN, MCZ, MHN, MNHN, NHMB, PSW.

Rhytidoponera wilsoni Brown

(Figs 27, 28, 33, 34)

Rhytidoponera wilsoni Brown, 1958, p. 294. Holotype worker, New Caledonia: Mt Mou 10.xii.1954 (E. O. Wilson acc. No. 110) (MCZ) [examined].

Worker measurements ($n = 10$). HW 1.04–1.10, WL 1.65–1.76, CI 0.87–0.90, MI 0.31–0.37, SI 1.00–1.05, SLI2 0.16–0.21, SSC 7–11, FSC 6–9 ($n = 10$).

Diagnosis of Worker

Similar to *koumensis* (q.v.) in relative body dimensions, except head, mandibles, and scapes relatively longer (compare CI, MI, and SI values) and petiolar node conspicuously compressed in lateral view. Subpetiolar process consisting of a broad keel with a short spiniform tooth. Occipital margin flat to weakly concave in full-face (dorsal) view. Occipital lobes a little more prominent than in *koumensis* or *numeensis*.

Mandibles finely striate. Dorsum of head rugostriate, becoming rugose on the posterior half. Mesosoma rugose to rugulose, becoming rugostriate laterally, not conspicuously overlaid with punctulate or striolate sculpture. Abdominal tergite III with dense, concentric, transverse striation; abdominal tergite IV with weak, concentric or arched-transverse striation. Fine, erect setae common on most parts of body. Brown to dark brown, with glinting reflections; legs, mandibles, and antennae a contrasting ferruginous brown.

Comments

The petiolar node and subpetiolar process of *wilsoni* are unlike those of any other New Caledonia species. Specific differences between *wilsoni* and other *numeensis* group species are detailed under *koumensis* and *numeensis*.

I have not seen any material of *wilsoni* beyond the original type series.

Ecology

R. wilsoni is known only from rainforest between about 200 and 300 m. Brown's (1958) summary of Wilson's field notes indicates that workers forage both on the ground and on foliage. A single nest was located under a stone.

Material Examined

Chapeau Gendarme, Yahoué, Mt Mou; Ciu, near Mt Canala, 300 m. In ANIC, MCZ, MHN.

The *pulchella* group

Rhytidoponera arborea, sp. nov.

(Figs 41, 42, 47, 48)

Rhytidoponera pulchella; Emery (nec Emery, 1883) 1914, p. 396 (partim).

Type Material

Holotype worker. New Caledonia: Col d'Amieu Stn, 360 m, 21°36'S., 165°48'E., 20.ii.1977, nest in cleft of rainforest tree, 10 m above ground (P. S. Ward acc. No. 2268) (ANIC Type No. 7580).

Paratype workers. A series of nidoparatype workers, same locality, date, and accession number (ANIC, BPBM, BMNH, MCZ, and PSW).

Non-paratypic material. Additional material from 6 other localities which is considered to be conspecific is listed below (under *Material Examined*).

Measurements

Holotype worker. HW 1.31, WL 1.96, CI 0.93, MI 0.34, SI 0.97, SLI2 0.20, SSC 9, FSC 0.

Paratype workers and other material. HW 1.14–1.32, WL 1.78–2.00, CI 0.86–0.92, MI 0.30–0.40, SI 0.98–1.12 ($n=20$), SLI2 0.18–0.21, SSC 7–10, FSC 0–2 ($n=9$).

Diagnosis of Worker

Anterior clypeal margin obtusely angulate. Frontal lobes expanded laterally and covering most of the antennal insertions; frontal carinae subparallel, converging to 85–90% of their maximum distance, the latter (FCD) $< \frac{1}{2}$ the head width (FCI 0.41–0.46). Head quadrate, longer than wide, the sides weakly convex; occipital margin flat or very slightly concave, in full-face (dorsal) view. Eyes protruding slightly in dorsal view, OI 0.22–0.27. In lateral view, the frons rounds evenly into the vertex, the occipital lobes protruding slightly (OLI 0.43–0.46, OLD 0.62–0.66). Pronotum relatively slender, PI 0.76–0.82. Promesonotal

suture distinct, obtusely V-shaped in dorsal view. Mesopropodeal impression indistinct; basal face of propodeum weakly differentiated from the declivitous face, the latter a little longer than the former, in lateral view. Inferior pronotal tooth well developed. Petiole as illustrated: node robust, somewhat rounded, with a short anterior peduncle (LPI 0.53–0.58; DNI 0.90–1.01; PNI2 0.44–0.50); subpetiolar process consisting of a long, spiniform tooth (SLI2 0.18–0.21; SPI 0.13–0.23).

Mandibles striate. Head predominantly rugose, the inter-rugal punctures smooth and shining. Mesosoma and petiolar node rugose with interspaces shining, and with some rugulose sculpture on the sides; rugae tending to show a transverse orientation on the propodeum. Abdominal tergite III with irregular, transverse striae, becoming rugostriate to rugulose anterolaterally. Abdominal tergite IV with weak, transverse, striolate-imbricate sculpture. Gastric tergites opaque to subopaque. Medium length, erect setae present on most parts of the body. Standing hairs sparse on the upper surface of the femora (FSC 0–2; HSC 0–6, nearly always on the apical half). Abdominal tergites III and IV with a distinct mat of appressed pubescence. Black, with dark brown mandibles, antennae, and legs; the apical funicular and tarsal segments a lighter, ferruginous brown.

Comments

In comparison with other *pulchella*-group species having a dense mat of appressed pubescence on the gastric tergites, *arborea* is either larger (HW > 1.10 in *arborea*, HW < 1.00 in *pulchella* and *insularis*) or differs in pilosity (*depilis* has little erect pilosity; *terrestris* is a little more setose than *arborea*). *R. arborea* and *terrestris* are rather similar, but the differences between them appear to be consistent. The occipital lobes are a little better developed in *arborea* (OLI 0.43–0.46 in *arborea*, 0.40–0.44 in *terrestris*) and not as far apart (OLD 0.62–0.66 in *arborea*, 0.66–0.71 in *terrestris*) (samples of 10 and 13 workers for *arborea* and *terrestris*, respectively). The scapes and femora of *arborea* have fewer standing hairs, as shown by the following ranges of setal counts (data on *pulchella* are included for comparison):

	<i>arborea</i>	<i>terrestris</i>	<i>pulchella</i>
SSC	7–10 (n=10)	10–18 (n=13)	2–14 (n=12)
FCS	0–2 (n=10)	1–15 (n=13)	0–3 (n=12)
HSC	0–6 (n=21)	8–19 (n=42)	0–8 (n=21)

Finally, *arborea* and *terrestris* occur sympatrically (Col d'Amieu; vicinity of Col de Hô), and they are substituted for alternate alleles at three allozyme loci (amylase, esterase, and glutamate oxaloacetate transaminase).

Ecology

R. arborea has been collected in rainforest, from 40 to 450 m elevation, where workers were observed foraging on low foliage and on the ground. The present records suggest that this species may favour arboreal nesting sites: one colony was located in a cavity of a living rainforest tree, 10 m above the ground; another was nesting in an epiphytic fern (*Asplenium*) growing on a large boulder.

Material Examined

Ngoyé, 200 m; Col d'Amieu Stn, 360 m; Col de Hô, 40 m; Aoupinié For. Reserve, 440 m; 3 km SW. Touho, 150 m, 400 m; Nepouis Val., Ouaté Dist., 450 m; Hieghène. In ANIC, BPBM, BMNH, MCSN, MCZ, MNHN, NHMB, PSW.

Rhytidoponera depilis, sp.nov.

(Figs 39, 40, 45, 46)

Type Material

Holotype worker. New Caledonia: Fausse Yaté Rivière 10 m, 22°10'S., 166°55'E., 26.iv.1980, foraging on low vegetation, rainforest (P. S. Ward acc. No. 4106) (ANIC Type No. 7581).

Paratype workers: (1) A series of 2 accessions from Fausse Yaté Rivière (P. S. Ward acc. Nos 4104, 4106) (ANIC, PSW). (2) A series of 2 accessions from 6 km SE. Touaourou, 10 m, 22°14'S., 167°00'E., 27.iv.1980, workers foraging on low vegetation and nesting in soil at base of sapling, rainforest (P. S. Ward acc. Nos 4130-1, 4131) (BMNH, MCZ, MNHN, PSW). (3) 2 workers, Touaourou, 20.x.1958 (B. Malkin) (BPBM).

Non-paratypic material: 1 worker, 'Oubatché' (Sarasin and Roux) (MHN). I suspect that this worker, which Forel presumably received from Emery, has been mislabelled. Oubatché is north-west of Hienghène, at the opposite end of the island to the type locality. It is possible that this specimen is the '*pulchella*' worker which Emery (1914, p. 396) referred to, and briefly described, from Yaté.

Measurements

Holotype worker. HW 1.24, WL 1.91, CI 0.91, MI 0.36, SI 1.05, SLI2 0.19, SSC 0, FSC 0.

Paratype workers. HW 1.18-1.24, WL 1.78-1.85, CI 0.89-0.92, MI 0.35-0.40, SI 1.01-1.05, SLI2 0.17-0.20, SSC 0, FSC 0 ($n=9$).

Diagnosis of Worker

Similar to *arborea* (q.v.) in relative body dimensions, sculpture, and colour. Eyes a little larger (OI 0.27-0.30). Occipital lobes broadly rounded and not protruding in lateral view. Pronotum averaging a little more slender than in *arborea* (PI 0.74-0.78). Petiolar node relatively narrow in dorsal view (PNI2 0.42-0.45). Subpetiolar process with a rather broad tooth (SPI 0.21-0.31). Rugose sculpture on head becoming longitudinally rugostriate on vertex, near the posterior margin. Inter-rugal punctures on pronotum becoming isolated on the sides, surrounded by irregular striate sculpture. Sculpture on petiolar node and abdominal tergite III finer than in *arborea* (rugulose on node; finely rugostriate to striate on abdominal tergite III). Erect pilosity sparse or absent on most of the upper body surface, lacking entirely on the legs and scapes; gastric tergites covered by a dense mat of appressed pubescence, which is multibranched on abdominal tergite IV.

Comments

This is a large, black, *pulchella*-group species which can be immediately recognized by the lack of erect hairs on most parts of the body and by the densely pubescent gastric tergites.

Ecology

R. depilis is known only from coastal rainforest (10 m elevation). Workers were observed foraging on low vegetation. Two colonies were collected: both were located in soil next to a small sapling, and had a distinctive nest entrance in the form of a clay turret constructed around the base of the sapling (as in Fig. 75).

Rhytidoponera insularis, sp.nov.

(Figs 53, 54, 59, 60)

Type Material

Holotype worker. New Caledonia: Baie d'Oupi, Ile des Pins, < 5 m, 22°38'S., 167°32'E.,

10.v.1980, foraging on low vegetation, rainforest (P. S. Ward acc. No. 4282-2) (ANIC Type No. 7582).

Paratype workers: (1) A series of 10 accessions from three localities on Ile des Pins: Baie d'Oupi (P. S. Ward acc. Nos 4282-2, 4285-1); Tribu de Touète, 10 m, 22°35'S., 167°31'E. (P. S. Ward acc. Nos 4276-2, 4278); Kuto Pen., 5 m, 22°40'S., 167°26'E. (P. S. Ward acc. Nos 4271, 4288, 4289, 4290, 4293-1, 4294-2) (ANIC, BPBM, BMNH, MCZ, MNHN, PSW). (2) 9 workers, Kuto Pen., Ile des Pins, 1.iv.1977 (W. L. Brown) (MCZ, PSW).

Measurements

Holotype worker. HW 0.88, WL 1.30, CI 0.88, MI 0.36, SI 0.97, SLI2 0.18, SSC 1, FSC 0.

Paratype workers. HW 0.81-0.96, WL 1.19-1.41, CI 0.87-0.92, MI 0.33-0.42, SI 0.94-1.04 ($n=23$); SLI2 0.17-0.21, SSC 0, FSC 0 ($n=9$).

Diagnosis of Worker

Anterior clypeal margin obtusely angulate. Frontal lobes expanded laterally and covering most of the antennal insertions; frontal carinae subparallel, converging to c. 85% of the maximum distance, the latter (FCD) c. $\frac{2}{3}$ of head width (FCI 0.40-0.44). Head quadrate, longer than wide, the sides weakly convex; occipital margin flat to very slightly concave, in full-face view. Eyes relatively large (OI 0.26-0.31) and protruding slightly in dorsal view. In lateral view, the frons rounds evenly into vertex, and the occipital lobes protrude slightly. Pronotum relatively slender, PI 0.75-0.82. Promesonotal suture distinct, varying from broadly rounded to weakly angulate in dorsal view. Mesopropodeal impression indistinct or lacking; basal face of propodeum poorly differentiated from the declivitous face, the latter about twice the length of the former and slightly concave in lateral view. Inferior pronotal tooth well developed. Petiole as illustrated: with relatively high, wide node (LPI 0.46-0.52; DNI 0.78-0.89; PNI2 0.45-0.52) and with spine-like subpetiolar process (SLI2 0.17-0.21; SPI 0.15-0.21).

Mandibles shining, with weak, obsolete striation. Head rugose to rugo-striate, the coarse inter-rugal punctures partly overlaid by weaker rugulae. Mesosoma dorsum rugose, becoming intermixed with finer, rugulose sculpture on the mesopleura; declivitous face of propodeum transversely rugostriate. Petiolar node rugulose. Abdominal tergite III with transverse, striolate-imbricate sculpture; this sculpture weaker on abdominal tergite IV and becoming obsolete on the posterior half. Gastric tergites covered with a dense mat of appressed pubescence (numerous, small piligerous punctures are associated with this pubescence). Fine, erect setae present on most parts of the body, relatively sparse on the mesosoma dorsum, legs and scapes. Head, mesosoma, and petiolar node dark brown; gaster, legs, mandibles, and antennae testaceous brown.

Comments

This is a small (HW < 1.00), brown *pulchella*-group species, with a dense mat of appressed pubescence on the gastric tergites, and a relatively sparse cover of erect setae on the body. Differences between *insularis* and the closely related *pulchella* are detailed in the key and under the description of *pulchella*.

Ecology

R. insularis appears to be restricted to coastal forest (*Araucaria* forest and littoral rainforest, between 5 and 10 m) on Ile des Pins. Workers were observed foraging on the ground and (more commonly) on low foliage. Nests (six records) were located in the soil, among cracks and crevices in coralline limestone, and were difficult to excavate.

Rhytidoponera litoralis, sp. nov.

(Figs 65, 66, 71, 72)

Type Material

Holotype worker. New Caledonia: 3 km N. Goro, 5 m, 22°16'S, 167°01'E., 26.iv.1980, nest in rotting log, rainforest (P. S. Ward acc. No. 4117) (ANIC Type No. 7584).

Paratype workers. (1) A series of 4 accessions from 3 km N. Goro (P. S. Ward acc. Nos 4116, 4117, 4118, 4129) (ANIC, BPBM, BMNH, MCZ, MNHN, PSW). (2) A series of 2 accessions from 6 km SE. Touaourou, < 5 m, 22°14'S., 167°00'E., 27.iv.1980 (P. S. Ward acc. Nos 4122-1, 4124) (ANIC, MCZ, PSW).

Non-paratypic material. Additional material believed to be conspecific with *litoralis* comes from Ile des Pins, Ile Maré, Ile Lifou, and Houailou on the north-east coast of the main island (see below under *Material Examined*).

Measurements

Holotype worker. HW 1.02, WL 1.52, CI 0.91, MI 0.37, SI 0.96, SLI2 0.15, SSC 13, FSC 7.

Paratype workers and other material. HW 0.95-1.11, WL 1.37-1.65, CI 0.86-0.92, MI 0.33-0.41, SI 0.91-1.01 ($n=47$); SLI2 0.15-0.17, SSC 4-21, FSC 0-10 ($n=17$).

Diagnosis of Worker

Similar to *insularis* (q.v.) in relative body dimensions and sculpture. Body size somewhat larger, and eyes relatively smaller (OI 0.23-0.27). Declivitous face of propodeum more or less straight, in lateral view. Subpetiolar process shorter and thinner than that of *insularis* (SLI2 0.15-0.17, SPI 0.10-0.17). Rugose sculpture of head and mesosoma less overlaid with finer rugulae or striae, the coarse inter-rugal punctures more strongly shining. Abdominal tergites III and IV strongly shining, with weak anterolateral striolae which become effaced on the posterior halves. Short, erect pilosity common on the upper body surface, including the scapes and femora. Appressed or decumbent hairs moderately dense on abdominal tergites III and IV, separated by about their lengths. Body dark ferruginous brown, with lighter legs, mandibles and antennae, which contrast moderately with the body.

Comments

R. litoralis is a brown *pulchella*-group species which can be recognized by the combination of: (1) largely smooth and shining gastric tergites, with a moderate density of appressed or decumbent hairs; (2) prevalence of short, erect pilosity on the body (SSC 4-21, FSC 0-10). Among other species with a conspicuously shiny gaster, *versicolor* has few or no appressed hairs on the gaster and the erect body hairs are notably longer than those of *litoralis*; *mimica* and *nitidiventris* have very little erect pilosity on the upper surfaces of the scapes and femora (SSC 0-2, FSC 0); and *luteipes* has longer erect body hairs, in addition to pale luteous appendages which contrast strongly with the dark body.

R. litoralis workers from the Loyalty Is differ from those on the 'mainland' (including Ile des Pins) as follows: they are lighter (and more variable) in body colour; they average larger in body size; erect body hairs are less abundant (e.g. SSC 4-9 and FSC 0-4 in a sample of eight workers from Ile Maré, compared with SSC 6-21 and FSC 5-10 in a sample of 10 workers from the mainland); and the fine, striate sculpture on abdominal tergites III and IV tends to be more extensively developed. As a matter of convenience, I am considering the Loyalty Is and mainland populations conspecific, since they are clearly more closely related to one another than to any other populations of New Caledonian *Rhytidoponera*. The degree of differentiation approaches that found between sympatric sibling species in the genus. For example, it is similar to the differences between *arborea* and *terrestris* in New Caledonia and between *confusa* Ward and *chalybaea* Emery in Australia (Ward 1980a).

Ecology

R. litoralis shows a strong association with coastal forests, having been collected only in littoral rainforest and in coastal *Araucaria* forest, from 5 to 80 m. This type of habitat is illustrated in Holloway (1979, pp. 61, 86). Workers forage both on the ground and on low vegetation. Nest-site records: ex rotten log (1), in soil among cracks in coralline limestone (3), in soil at base of sapling, with clay turret nest entrance (2).

Material Examined

Ile des Pins and main island: Kuto Pen., Ile des Pins, 5 m; Ouro, Ile des Pins, 5 m; 3 km N. Goro, 5 m; 6 km SE. Touaourou, < 5 m; Houailou. **Loyalty Is:** 3 km SE. Tawainèdre, Ile Maré, 5 m, 50 m, 70 m, 80 m; 2 km W. Tawainèdre, Ile Maré, 30 m; Tadine, Ile Maré; Cap des Pins, Ile Lifou. In ANIC, BPBM, BMNH, MCZ, MNHN, PSW.

Rhytidoponera luteipes, sp. nov.

(Figs 51, 52, 57, 58)

Type Material

Holotype worker. New Caledonia: Col de Hô, 40 m, 21°11'S., 165°31'E., 5.v.1980, nest in soil at base of sapling, rainforest (P. S. Ward acc. No. 4235) (ANIC Type No. 7585).

Paratype workers, 1 male. (1) A series of 3 accessions from Col de Hô (P. S. Ward acc. Nos 4235, 4238, 4240) (ANIC, BPBM, BMNH, MCZ, MNHN, PSW); (2) A series of 2 accessions from Aoupinié For. Reserve, 440 m, 21°09'S., 165°19'E., 18.iv.1980 (P. S. Ward acc. Nos 4049, 4051-2) (ANIC, MCZ, PSW).

Non-paratypic material. Additional material from three other localities which is believed to be conspecific with *luteipes* is listed below (under *Material Examined*).

Measurements

• **Holotype worker.** HW 0.83, WL 1.19, CI 0.88, MI 0.36, SI 1.00, SLI2 0.14, SSC 6, FSC 0.

Paratype workers and other material. HW 0.80-0.98, WL 1.19-1.45, CI 0.85-0.91, MI 0.33-0.40, SI 0.96-1.06 ($n=39$); SLI2 0.12-0.16, SSC 3-15, FSC 0-4 ($n=14$).

Diagnosis of Worker

Similar to *insularis* (q.v.) in relative body dimensions and sculpture. Frontal carinae almost parallel, converging posteriorly to 90-95% of their maximum distance. Occipital margin flat in full-face view. Eyes averaging a little smaller than *insularis* (OI 0.23-0.29). Basal face of propodeum poorly differentiated from the declivitous face, the latter more or less straight in lateral view. Anterior peduncle of petiole well developed; subpetiolar process relative short; petiolar node rather narrow in dorsal view (PNI2 0.40-0.48). Mandibles finely striate. Pronotum areolate-rugose, the interspaces large and shining; remainder of mesosoma as in *insularis*, except less intermixed with finer rugulose sculpture. Abdominal tergite III with fine, concentrically transverse striation, which is partly effaced medially. Abdominal tergite IV largely smooth and shining, at most weakly striolate on the anterior half and lateral margins. Fine, erect setae common on most parts of the body, including the scapes and legs. Appressed and decumbent hairs present on abdominal tergites III and IV, but varying widely in abundance (sparse to very dense). Body dark brown to black, with contrasting pale luteous legs (including coxae), mandibles, and antennae.

Comments

In addition to the unique coloration (pale luteous appendages contrasting with dark body), characteristic features of *luteipes* are: a relatively short subpetiolar process (SLI2 0.12-0.16), areolate-rugose pronotum, and abundant erect pilosity (SSC 3-15, FSC 0-4).

No other species with appressed or decumbent hairs on the gastric tergites displays this combination of characters.

There is considerable variation in the density of these appressed gastric hairs among the type material of *luteipes*, including workers from the same nest. The holotype worker shows an intermediate condition of density (Fig. 58). In workers from populations farther north (near Touho and Hienghène), the appressed hairs form a dense, pubescent mat, similar to that seen in *insularis* or *pulchella* (e.g. as in Fig. 62), and the striae on the gastric tergites are better developed. Workers from near Hienghène also tend to have infuscated femora which contrast with the paler coxae, tibiae and tarsi. Finally, specimens from the northernmost locality (Roches d'Ouaïème) have less dense pubescence on the gastric tergites and a shiny, testaceous brown gaster which contrasts with the black head and mesosoma.

Ecology

R. luteipes was collected in several rainforest sites (mostly gully rainforest and rainforest edges) and in one montane rainforest locality (Roches d'Ouaïème) at altitudes ranging from 40 to 750 m. Workers were observed foraging only on low vegetation, and all nests (5 records) were directly in the soil at the base of a sapling, with a clay turret nest entrance.

Material Examined

Col de Hô, 40 m; Aoupinié For. Reserve, 440 m; 3 km SW. Touho, 270 m, 400 m; 9 km SW. Hienghène, 140 m; Roches d'Ouaïème, 750 m. In ANIC, BPBM, BMNH, MCZ, MNHN, PSW.

Rhytidoponera mimica, sp. nov.

(Figs 67, 68, 73, 74)

Type Material

Holotype worker. New Caledonia: Col d'Amoss, 300 m, 20°18'S., 164°25'E., 3.v.1980, foraging on low vegetation, gully rainforest (P. S. Ward acc. No. 4215-1) (ANIC Type No. 7586).

Paratype workers. A series of 3 accessions from the type locality, same date (P. S. Ward acc. Nos 4215-1, 4216, 4217) (ANIC, BPBM, BMNH, MCZ, MNHN, PSW).

Measurements

Holotype worker. HW 0.90, WL 1.34, CI 0.88, MI 0.40, SI 1.06, SLI2 0.18, SSC 0, FSC 0.

Paratype workers ($n = 9$). HW 0.86-0.92, WL 1.22-1.34, CI 0.87-0.90, MI 0.36-0.44, SI 0.99-1.07, SLI2 0.15-0.18, SSC 0-1, FSC 0.

Diagnosis of Worker

Similar to *insularis* in relative body dimensions and sculpture. Anterior clypeal margin more sharply angulate. Petiole with a relatively high, narrow node (LPI 0.45-0.49; DNI 0.86-0.90; PNT2 0.39-0.43), and with a conspicuous anterior peduncle and a slender, spine-like subpetiolar process (SPI 0.13-0.18). Head rugose to longitudinally rugostriate, the inter-rugal spaces shining. Mesosoma rugose to transversely rugostriate, the rugae weak and interspaces smooth and shining. Anepisternum largely smooth and shining, and devoid of sculpture centrally except for 2 or 3 punctures. Abdominal tergites III and IV shining, with weak striolate sculpture which is posteromedially obsolete. Gastric tergites with appressed hairs moderately dense, separated by about their lengths. Erect setae relatively sparse on most parts of the body, generally lacking on the propodeum and upper surfaces of the scapes and femora. Mesosoma and petiole dark brown to black; head a contrasting light ferruginous brown; gaster, legs (including coxae) and mandibles a paler luteous brown, contrasting strongly with the mesosoma.

Comments

Workers of *mimica* have a unique and divergent coloration pattern among the New Caledonian *Rhytidoponera*. The conspicuous orange and black pattern is shared with workers of a sympatric foliage-foraging *Camponotus* species (cf. *croceomaculatus* Emery). This may be a case of Mullerian, rather than Batesian, mimicry since: (1) *Rhytidoponera* workers can inflict a painful sting; (2) elsewhere in New Caledonia, *Rhytidoponera* species with a conspicuous shiny gaster, such as *versicolor*, appear to be mimicked by various foliage-frequenting arthropods (see below under *Patterns of Ecological Divergence*).

Coloration aside, *mimica* may be distinguished from other congeners by the combination of small size (HW < 0.95 mm), absence of erect pilosity from the propodeum and upper surfaces of the femora, and absence of dense pubescence on the shiny gastric tergites.

Ecology

R. mimica was collected in a small patch of gully rainforest, 300 m elevation, surrounded by niaouli (*Melaleuca* scrub). Similar habitat is depicted in Holloway (1979, p. 123). Workers were foraging on low vegetation. Two nests were located, both in vertical banks of soil beside a stream.

Rhytidoponera nitidiventris, sp. nov.

(Figs 63, 64, 69, 70)

Type Material

Holotype worker. New Caledonia: Grottes de Koum, 40 m, 20°32'S., 164°20'E., 3.v.1980, nest in soil at base of sapling, rainforest (P. S. Ward acc. No. 4206) (ANIC Type No. 7587).

Paratype workers. A series of 2 accessions from the type locality, same date (P. S. Ward acc. Nos 4205, 4206) (ANIC, BPBM, BMNH, MCZ, MNHN, PSW).

Measurements

Holotype worker. HW 1.10, WL 1.59, CI 0.90, MI 0.35, SI 0.95, SLI2 0.17, SSC 0, FSC 0.

Paratype workers. HW 1.05–1.14, WL 1.53–1.64, CI 0.90–0.93, MI 0.32–0.38, SI 0.94–0.96, SLI2 0.16–0.17, SSC 0–2, FSC 0 ($n=9$).

Diagnosis of Worker

Similar to *arborea* (q.v.) in relative body dimensions, sculpture, and colour. Frontal carinae almost parallel, converging posteriorly to 90–95% of their maximum distance. Eyes a little larger than those of *arborea* (OI 0.27–0.30). Occipital lobes broadly rounded and non-protruding, in lateral view. Promesonotal suture distinct, broadly and evenly rounded in dorsal view. Basal face of propodeum weakly differentiated from declivitous face, the latter about twice as long as the former, in lateral view. Petiole more slender than that of *arborea* (LPI 0.45–0.51, DNI 0.78–0.86), with a shorter subpetiolar process (SLI2 0.16–0.17). Rugose sculpture of head showing a more distinct longitudinal orientation, particularly on the vertex. Coarse punctures on sides of mesosoma intermixed with finer rugulae. Petiolar node rugulose. Abdominal tergite III transversely striate, with conspicuous, elongate, piligerous punctures. Abdominal tergite IV with weak transverse striae, becoming effaced and shining on the posterior half. Both appressed and erect or suberect hairs common on the gastric tergites, the appressed hairs separated by about their lengths and not forming a dense pubescent mat. Fine, erect hairs common on the petiolar node, mesosoma dorsum, and head; rather sparse on the scapes and legs (SSC 0–2, FSC 0). Dark brown to black, the apices of the funiculi, tarsi, and mandibles a paler testaceous brown.

Comments

R. nitidiventris is a relatively large, dark, *pulchella*-group species which can be recognized by a unique combination of large size (HW > 1.00), scarcity of standing hairs on the scapes and femora (SSC 0–2, FSC 0), and absence of a dense mat of appressed pubescence on the gastric tergites.

Ecology

The type locality is a patch of rather dry rainforest, on limestone [illustrated by Holloway (1979, p. 120)]. Workers were foraging on low vegetation, and a nest was located in soil at the base of a sapling, with a characteristic clay turret nest entrance.

Rhytidoponera pulchella (Emery)

(Figs 55, 56, 61, 62)

Ectatomma pulchellum Emery, 1883, p. 149. Holotype worker, New Caledonia (MCSN) [examined].

Rhytidoponera pulchella (Emery); Brown, 1958, p. 291 [partim].

Worker measurements. HW 0.80–0.96, WL 1.19–1.42, CI 0.85–0.91, MI 0.31–0.38, SI 0.92–1.06 ($n=21$); SLI2 0.19–0.21, SSC 2–14, FSC 0–3 ($n=12$).

Diagnosis of Worker

Similar to *insularis* (q.v.) in relative body dimensions and sculpture. Declivitous face of propodeum more or less straight in lateral view. Subpetiolar process a little more slender, on average (SPI 0.12–0.17). Mandibles more densely striate. Abdominal tergite III concentrically striate, abdominal tergite IV with weaker, striolate-imbricate sculpture, which becomes effaced towards the posterior margin. Fine, erect setae common on most parts of the body. Dark brown to black, the mandibles, antennae, and legs a little lighter; funicular and tarsal segments paler, testaceous brown.

Comments

The distinctive features of *pulchella* are small size (HW < 1.00), densely pubescent gastric tergites, and a dark, unicolored body. The otherwise similar *insularis* has a bicolored body, and a rather sparse cover of erect hairs (differences detailed in key). *R. pulchella* may be distinguished from *luteipes* by its larger eyes (OI 0.28–0.32 in *pulchella*, 0.23–0.29 in *luteipes*), longer subpetiolar process (SLI2 > 0.18 in *pulchella*), and lack of strongly contrasting appendages. In addition, not all *luteipes* workers possess a dense mat of appressed pubescence on the gastric tergites. *R. pulchella* differs from *terrestris* in size, pilosity (see discussion under *arborea*), and details of sculpture. The petiolar node of *pulchella* is generally more slender (shorter and higher) than that of *terrestris*, but there is sufficient variation in both species to produce considerable overlap in LPI values (0.45–0.54 in *pulchella*, 0.49–0.59 in *terrestris*) and DNI values (0.77–0.95 in *pulchella*, 0.84–1.00 in *terrestris*).

Ecology

R. pulchella appears to be localized in patches of rainforest from 40 to about 200 m elevation, in the southern part of New Caledonia. At Kuenthio Rivière, workers were observed foraging predominantly on low vegetation, and nesting in soil at the base of small saplings (4 records). There is also one record of a nest under a stone.

Material Examined

'N. Caléd.' [holotype]: Chapeau Gendarme (Yahoué): Yahoe, 12 km N. Nouméa; Mt Mou; Col de la Pirogue; Kuentio R., 14 km SW. Thio, 40 m. In ANIC, BMNH, MCSN, MCZ, PSW.

Rhytidoponera terrestris, sp. nov.

(Figs 43, 44, 49, 50)

Rhytidoponera pulchella, Brown (nec Emery), 1958, p. 291 (partim).

Type Material

Holotype worker. New Caledonia: Toma R., Col d'Amieu For. Stn. 380 m, 21°35'S., 165°46'E., 23.ii.1977, nest in soil, rainforest (P. S. Ward acc. No. 2316) (ANIC Type No. 7589).

Paratype workers, one male. (1) A series of 2 accessions from the type locality, same date (P. S. Ward acc. Nos 2315, 2316) (ANIC, BPBM, BMNH, MCZ, MNHN, PSW). (2) 3 workers from Table Unio, 740 m, 21°34'S., 165°46'E., 22.ii.1977, foraging on palm leaf, rainforest (P. S. Ward acc. No. 2313) (ANIC, PSW).

Non-paratype material. A long series of collections from 14 other localities in southern New Caledonia, plus one questionable record from Vanuatu (see below under *Material Examined*).

Measurements

Holotype worker. HW 1.00, WL 1.54, CI 0.88, MI 0.40, SI 1.02, SLI 0.19, SSC 12, FSC 8.

Paratype workers and other material. HW 1.04–1.32, WL 1.54–1.94, CI 0.87–0.96, MI 0.32–0.40, SI 0.90–1.04 ($n=41$); SLI 0.18–0.21, SSC 10–18, FSC 1–15 ($n=12$).

Diagnosis of Worker

Agreeing closely with *arborea* (q.v.) in relative body dimensions, sculpture, and colour. Eyes averaging a little larger (OI 0.26–0.30). Occipital lobes less developed posteromedially (OLI 0.40–0.44; OLD 0.66–0.71). Promesonotal suture distinct, tending to be more evenly rounded in dorsal view. Rugose sculpture on cranium becoming rugostriate at the posterior margin so that the rugae on the vertex show a clearer longitudinal orientation than in *arborea*. Abdominal tergite III transversely striate to rugostriate, the sculpture finer than in *arborea*. Standing hairs common on upper surfaces of femora (FSC 1–15; HSC 8–19, usually including some standing hairs on the distal half). Scares more pilose than those of *arborea* (SSC 10–18). Appressed pubescence common on abdominal tergite IV, less dense on abdominal tergite III.

Comments

R. terrestris is a relatively large, dark species, with abundant erect pilosity and with appressed pubescence on the opaque gastric tergites. Among other large, dark species in the *pulchella* group, *nitidiventris* is essentially devoid of standing hairs on the scapes and upper surface of the fore femur, and has a shiny gaster with sparser pubescence; *depilis* lacks erect pilosity on most of the body and possesses an exceptionally dense mat of appressed pubescence on both gastric tergites; and *arborea* has shorter and less dense pilosity than *terrestris* (see diagnosis of *terrestris* worker and discussion under *arborea* for details of these and other differences with *arborea*).

R. terrestris may be distinguished from the remaining *pulchella*-group species by its large size and dark coloration, in addition to more specific characters mentioned in the key.

Ecology

R. terrestris is one of the more common *pulchella*-group species and has been collected in littoral forest and in upland rainforest, from 5 to 740 m elevation. Workers forage predominantly on low vegetation. Nest-site records: in soil at base of sapling, with turreted nest entrance (7 records), in soil without turret (3 records), and under stone (1 record).

Material Examined

Baie d'Oupi, Ile des Pins, < 5 m; Tribu du Touëté, Ile des Pins, 10 m; 2 km SE. Ouaméo, Ile des Pins, 70 m; Kuto Pen., Ile des Pins, 5 m; Gadji, Ile des Pins, < 5 m; Mt Koghis, 350 m, 650 m; Col de Tongoué; Nouméa; Mt Mou; Kuenthio Riv., 14 km SW. Thio, 40 m; Ciu, near Mt Canala, 300 m; La Crouen, 130 m; Koh; Toma R., Col d'Amieu For. Stn, 380 m; Table Unio, 740 m; Hô R., 5 m. In ANIC, BPBM, BMNH, MCZ, MNHN, PSW.

In the BMNH there are two *terrestris* workers labelled 'New Hebrides/J.J. Walker/1904-168'. If valid, this represents the only record of the genus *Rhytidoponera* from Vanuatu. Given that *terrestris* is a typical member of a group of endemic New Caledonian species, it seems likely that the two workers have been mislabelled or represent a relatively recent introduction.

Rhytidoponera versicolor Brown

(Figs 19, 20, 25, 26)

Rhytidoponera versicolor Brown, 1958, p. 292. Holotype worker, New Caledonia: Montagne des Sources, 17.xii.1954 (E. O. Wilson acc. No. 185) (MCZ) [examined].

Worker measurements. HW 0.75-1.08, WL 1.15-1.51, CI 0.83-0.94, MI 0.32-0.40, SI 0.92-1.09 ($n=48$); SLI2 0.16-0.19, SSC 6-21, FSC 0-15 ($n=18$).

Diagnosis of Worker

Similar to *insularis* (q.v.) in relative body dimensions and sculpture. Frontal carinae subparallel, converging to c. 90-95% of their maximum distance. Eyes averaging smaller than those of *insularis* (OI 0.21-0.29). Declivitous face of propodeum straight or weakly concave, in lateral view. Subpetiolar process averaging a little shorter than that of *insularis* (SLI2 0.16-0.19). Mandibles finely striate. Rugose sculpture of head and mesosoma less overlaid with rugulose or striate sculpture, the inter-rugal punctures large and shining, particularly on the pronotum. Petiolar node rugose. Abdominal tergites III and IV mostly smooth and strongly shining, with weak anterolateral striolation (and scattered piligerous punctures). Appressed and decumbent hairs scarce or lacking on the gastric tergites. Erect pilosity abundant on the body, scapes, and legs; the setae of variable length with the longest considerably greater than the eye diameter (ED). Head, mesosoma, and petiole dark brown to black, with contrasting ferruginous brown legs, mandibles, and antennae. Gaster varying from dark brown to a contrasting rich ferruginous brown (as in the holotype).

Comments

R. versicolor may be characterized by the smooth and strongly shining gastric tergites which are devoid of appressed hairs or nearly so. Two other *pulchella*-group species with shiny gasters (*litoralis* and *luteipes*) may have some workers which approach *versicolor* in the sparseness of these appressed hairs. However, *litoralis* has a less dense covering of erect setae on the body dorsum (compare Figs 20, 66), and the longest setae do not exceed the eye diameter (ED). In *luteipes*, abdominal tergite III is more densely striate and the subpetiolar process is shorter (SLI2 0.12-0.16).

There is notable variation among *versicolor* populations. Workers exhibit differences in sculpture (particularly the amount of striolation on abdominal tergite III), pilosity (variable

numbers of appressed hairs on the gastric tergites), petiole shape, body size, and colour. The gaster ranges in colour from a rich orange-brown to dark brown, thus contrasting variably with the remainder of the body. These differences occur on a local scale: at Montagne des Sources the *versicolor* population at 560 m in gully rainforest with emergent *Araucaria bernieri* (illustrated by Holloway, (1979, p. 62)) has predominantly light-gastered workers, while 3 km farther north (and 220 m higher) the *versicolor* population in a stand of *Araucaria muelleri* (see Holloway 1979, p. 102) is entirely dark-gastered. (Incidentally, the Montagne des Sources altitudes of '800 m' and '1000 m' cited by Brown (1958) for Wilson's collections of light- and dark-gastered workers, respectively, appear to be inaccurate.)

Although it is typical for *versicolor* workers to have light, ferruginous brown appendages which contrast with a black head and mesosoma (regardless of the colour of the gaster), two workers from St Louis Mission both have a ferruginous brown head and mesosoma, which contrast only modestly with the paler appendages and gaster, and workers from 6 km south-east of Touaourou are unicolorous black, with non-contrasting, dark brown legs!

Ecology

R. versicolor has been recorded from a variety of habitats (littoral forest, rainforest, montane rainforest, and open woodland) between 10 and 780 m elevation. This species appears to be restricted to sites on, or near, ultramafic soils in the south end of New Caledonia. Workers forage predominantly on low vegetation. Nest-site records: directly in soil (2), in soil next to sapling, with turreted nest entrance (2), under stone (1), ex rotten wood fragment (1).

Material Examined

6 km SE. Touaourou, 10 m; 2 km SW. Yaté-Village, 400 m; Mt Ouénarou, 300 m; Col de Mouirange, 240 m; Rivière Bleue, 170 m, 370 m; Mt des Sources, '800 m' [sic], '1000 m' [sic], 460 m, 560 m, 780 m; St Louis Mission, 120 m; Koghis Cascade, 650 m. In ANIC, BPBM, BMNH, MCZ, MHN, MNHN, PSW.

Discussion

Patterns of Ecological Divergence

The evolutionary radiation which has occurred among the New Caledonian *Rhytidoponera* (especially within the *pulchella* group) has no counterpart among congeners on the Australian mainland. While there are certainly species-rich groups in Australia, one never finds so many closely related species in such a small geographical area (400 by 50 km). This difference might reflect the rugged topography and patchy distribution of suitable habitats on New Caledonia, coupled with ecological opportunities provided by a disharmonic (taxonomically unbalanced) ant fauna. On the other hand there is no evidence of 'ecological release' into strikingly different adaptive zones. Field observations indicate that the New Caledonian *Rhytidoponera* are generalized predators and scavengers (as they are in Australia). This is also suggested by the relatively homogeneous habitus (body shape) of workers, especially the uniform size and shape of the mandibles.

Unlike the Australian species of *Rhytidoponera*, those on New Caledonia are more or less restricted to mesic forest, and they have not penetrated the xeric, *Melaleuca*- and *Acacia*-dominated scrub habitats on the island. Within the mesic environments which have been occupied, there is some habitat specificity. Thus, *acanthoponeroides* is found primarily in montane rainforest, *versicolor* is confined to ultramafic sites, and several species occur only in coastal forest. Such habitat specialization is not prevalent throughout entire species-groups, however.

The only clear ecological adaptation which characterizes an entire species-group is the foliage-foraging habit of the members of the *pulchella* group. Workers in this group of species were observed foraging predominantly on low vegetation (85 out of 96 foraging records), in

contrast to the other New Caledonian *Rhytidoponera*, in which workers were observed foraging exclusively (*koumensis*, *numeensis*, and *acanthoponeroides*) or predominantly (*fulgens* group) on the ground. Associated with these differences in foraging behaviour, most species in the *pulchella* group nest directly in the soil, often at the base of a small sapling around which a characteristic nest entrance is constructed in the form of a clay turret (Fig. 75). Such a nest entrance apparently provides ready access to the understorey or forest edge vegetation. This nest architecture is not known to occur in any other *Rhytidoponera* species, but it has been observed in a foliage-foraging species of the neotropical ectatommine genus *Acanthoponera* (J. Longino, personal communication).

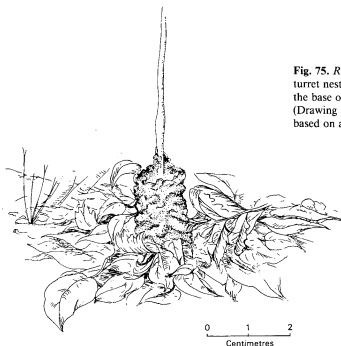
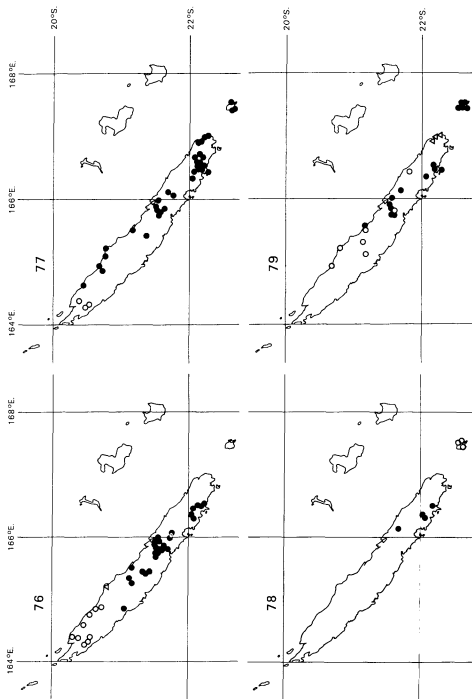


Fig. 75. *Rhytidoponera versicolor* clay turret nest entrance, moulded around the base of a rainforest sapling. (Drawing by Alyne Lavoie-Ruppanner, based on an original photograph.)

At least some of the *pulchella*-group species (*mimica*, *versicolor*) appear to be involved in localized, mimicry complexes with other endemic ants (*Tetramorium tenuicrinis* Emery, *Chelaner* spp. and *Camponotus* spp.) and with other foliage-foraging arthropods (including spiders and female-brachypterous torymid wasps) (Ward, unpublished observations). Presumably the predators driving this system are birds or endemic lizards (Gekkonidae and Scincidae). The localized variation in arthropod colour patterns suggests a viscous population structure on the part of the predators.

Speciation Patterns

A striking feature of the genus *Rhytidoponera* in New Caledonia is the existence of all degrees of differentiation among closely related, allopatric populations. On the one hand, there are relatively homogeneous species, such as *numeensis* and *pulchella*, in which most populations show rather limited morphological differentiation. At the other extreme are such taxa as *opaciventris* and *versicolor*, which exhibit marked interpopulation variation in sculpture, pilosity, and/or colour. Morphological (and allozymic) differentiation among populations of these variable taxa (e.g. between Loyalty Is and mainland populations of *litoralis*, or among *opaciventris* populations from different geographical areas) is not qualitatively different from that which is observed between closely related species. Indeed,



Figs 76-79. Distribution of closely related pairs or triplets of *Rhytidoponera* species in New Caledonia: 76, *R. fulgens* (●), *R. opaciventris* (○) and *R. aquila* (△); 77, *R. numeensis* (●) and *R. koumensis* (○); 78, *R. pulchella* (●) and *R. insularis* (○); 79, *R. terrestris* (●), *R. arborea* (○) and *R. depilis* (△).

there are no non-arbitrary criteria for the assignment of specific or infraspecific status to such variably differentiated, allopatric entities.

Closely related pairs or triplets of species tend to be distributed allopatrically along a gradient from south-east to north-west (Figs 76–79), although two sibling species (*arborea* and *terrestris*) have sympatric populations. The distribution patterns are presumably the result of historical geographical barriers, mostly orthogonal to the long axis of the island, combined with limited dispersal capabilities in the isolated populations due to the absence of winged females.

Overall, the patterns of differentiation support the notion that speciation in New Caledonian *Rhytidoponera* is essentially an allopatric process. Moreover, the finely graded degrees of differentiation are incompatible with the view that speciation occurs in a punctuated fashion.

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	1	6	7	1	7	7	3	2	6	1	1	6	3	4	2	3	3
Superoxide dismutase-1 (SOD-1)	1-92	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
	1-83						+										
	1-00			+			+					+					
Malate dehydrogenase (MDH)	1-07																
	0-85	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Malic enzyme (ME)	1-00	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
	0-95		(+)														
Phosphoglucosylase (PGM)	1-15																
	1-00						+					+					
	0-84	+															
	0-72		+	+		(+)											
	0-54					(+)											
Leucine aminopeptidase (LAP)	1-00						+			+	+	+	+	+	+	+	+
	0-81	+	+	+	+	+											
	0-65	+															
Glutamate oxaloacetate transaminase (GOT)	1-27	+					+			+	+	(+)					
	1-12		+	+	+	+	+					(+)					
	1-00													+			
Isocitrate dehydrogenase (IDH)	1-18	+	+	+	+	+	+							+			
	1-00		+				+			+	+	+	+	+	+	+	+
Lactate dehydrogenase (LDH)	1-45	+															
	1-34													+			
	1-16		+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
No. of colonies sampled/per locus	1	6	7	1	7	7	3	2	6	1	1	6	3	4	2	3	3